Lateglacial and Middle Holocene Coleoptera assemblages from coastal environments in South-Western Sweden

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Ninety-eight insect taxa were recorded in lagoon deposits at a site in SW Sweden. Remains of beetles totally dominate the insect assemblages. The bottom peat, which dates to ca. 10,300 BP consists of insect remains belonging to an arctic/alpine fauna. The upper peats and gyttja, that were deposited during the Middle Holocene (ca. 7,800 to 5,100 BP), during the Tapes transgression, contain temperate species. The majority of these species are found in southern Sweden today. However, a portion of the species in the fossil assemblages have not previously been recorded from the province of Halland and in several cases not in the entire area of southern Sweden either. The results suggest a relatively high faunal diversity and a spectrum of habitats within this lagoon environment, which probably has no modern analogue in S. Sweden today. The reasons for the extinction of species in the study area are discussed, including changes in climate and local environment.

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Introduction

In connection with excavation work for a new railway at Moarna, near the village of Tvååker, 10 km south-east of Varberg in the province of Halland, SW Sweden, clayey sediments and peat were exposed (Fig. 1). Samples taken from the bottom clay, upper clayey gyttja and peat layers were analysed. Macroscopic remains of plants and mollusc shells indicated that the gyttja and peat were of limnic/brackish origin, whereas the bottom clay was deposited in a marine environment. Based on the stratigraphic information from this brief survey and earlier studies (Mörner 1969, Påsse 1990) together with geomorphological features, it was concluded that the exposed section was a part of an ancient lagoon. Similar basins are rather frequent along the coast of Halland. Many of these lagoons were formed during the Early Holocene by a period of sea-level rise (the Tapes transgression). The limnic sedimentation often ceased when the sea-level began to drop around 6,000 BP (Mörner 1969, Påsse 1983,1990).

In addition to macroscopic plant remains and shells, subfossil insects were abundant in the gyttja and peat samples. We thus decided to carry out a more systematic palaeoentomological study at the site, so the section was resampled and dated. Palaeoecological studies, including insect analyses, on contemporary deposits from lagoonal sites along the coast of the Baltic Sea in southernmost Sweden have demonstrated the high diversity of the flora and fauna that characterised this type of environments (Lemdahl 1988a, Gaillard et al. 1988, Gaillard & Lemdahl 1994). In the paper we present and discuss the fossil beetle record from the investigated site at Moarna.

Study area and site

The basin of the ancient lagoon is situated less than 5 km from the present shoreline of the Kattegatt Sea (Fig. 1). The area is dominated by sandy clayey deposits with a thickness that sometimes

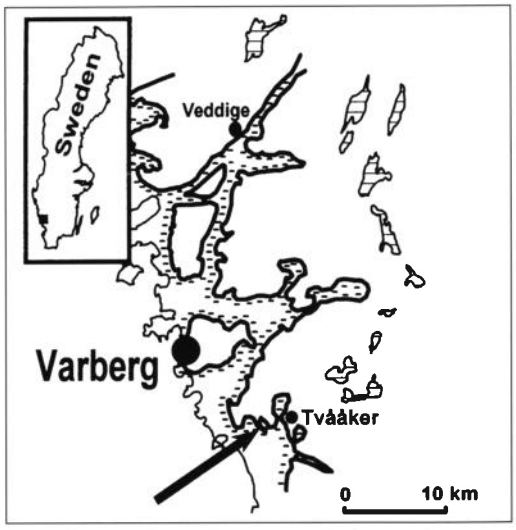

Fig. 1. Map of the study area, situated in south-western Sweden (insert map). The bold line indicates the shore line during the Tapes trangression maximum. The sampled ancient lagoon site at Moarna is indicated by the bold arrow.

Karta som visar undersökningsområdet i Halland, sydvästra Sverige (infälld karta). Tjock linje visar den forntida strandens läge under Tapestransgressionens (mellan ca 8000-6000 år sedan (BP)) maximala nivå. Pilen pekar på den undersökta forntida lagunen.

exceeds 35 m. The Quaternary deposits cover a Precambrian bedrock of granitic gneiss, which is exposed as outcrops directly east of the basin, where thin deposits of till are also found. West of the basin the area is dominated by sand dunes, probably mainly of postglacial origin.

The climate in the region today is rather oceanic with a mean July temperature around 17°C and a mean January temperature of ca. -1°C. The annual precipitation is around 600 mm (Raab and Vedin 1995). The study area is situated in the Northern Temperate vegetation zone (Ahti et al. 1968) and the vegetation at the site today is dominated by a grass-rich pine forest.

The lithology of the studied section is shown in Fig. 2. In the bottom silty clay (layer 7) no macroscopic remains of plants or animals were found. It was probably deposited during the period when the area was deglaciated. The bottom peat (layer 6) includes remains of plants, such as *Betula nana, Dryas octopetala, Carex* spp., *Ranunculus* (s.g. *Batrachium*) spp., and *Potamogeton*. The lower part of the slightly gyttja clay (layer 5) is rather rich in mollusc shells of species such as *Cardium edule* (L.), *Mytilus edulis* L., *Littorina littorea* (L.) and *Hydrobia* sp., while shells are very rare in the upper part. This suggests that the clay was deposited in marine or brackish water, probably during the Tapes transgression. The carr peat (layer 4) may have been formed during a shorter period with a lower sea level. The peat is composed mainly of remains of *Phragmites* and wood pieces. In layer 3, the clay gyttja, mollusc shells of the species mentioned above were recorded in the lowermost part, while in the upper part no shells were found. Macroscopic remains of vascular plants such as *Ruppia, Zannichellia* and *Chenopodium* spp. are also abundant in the gyttja, especially in the uppermost part. This suggests that the gyttja was deposited in brackish water. The upper reed peat (layer 2), dominated by *Phragmites* remains, may have began to form after the regression of the sea. The gyttja and peat deposits are covered by about one metre of aeolian sand.

Methods and material

Samples for insect analysis were disaggregated in a 10% sodium carbonate solution and washed through a sieve with 0.25 mm mesh. The insect remains were sorted out under a binocular microscope at low magnification. The identifications of the remains were carried out by using keys for modern specimens and by comparison with modern specimens from reference collections. The determinations are mainly based on complete body parts or fragments of heads, thoraces and elytra. In a number of cases, such as *Badister* cf. *dorsiger*, *Helophorus* cf. *arvernicus, Simplocaria* cf. *elongata* and *Galerucella* cf. *grisescens* (Tab. 1) the fossil remains resembles the modern specimens very much, however, we are not able to confirm the identifications with certainty. Minimum numbers of individuals for each taxon and sample are calculated from the most abundant skeletal part. For further details concerning the methods of insect analysis, readers are referred to e.g. Coope (1986), Lemdahl (1988b) or Elias (1994).

The chronostratigraphy of the sampled section was established on the basis of three radiocarbon

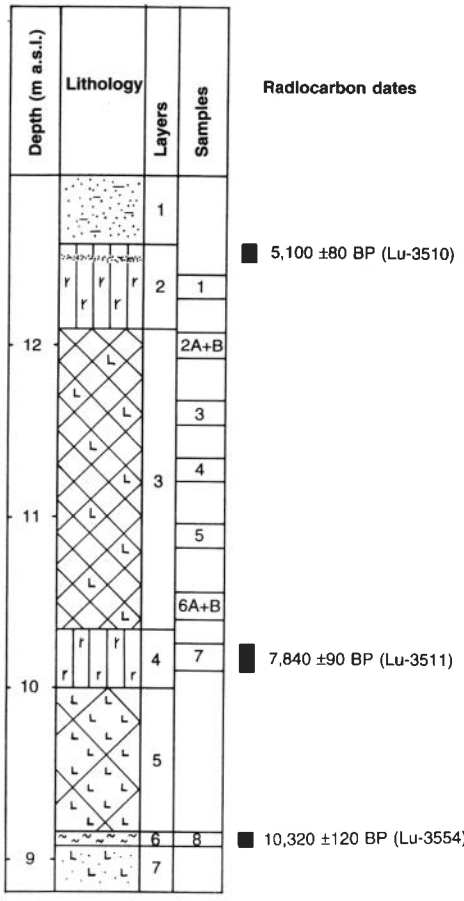

Fig. 2. The studied section from the ancient lagoon at Moarna, Tvåker, SW Sweden. Lithology, sampling and radiocarbon dates are indicated. Depth in metres above sea level. The lithology is illustrated by symbols commonly and the exposed layers consist of (1) slightly silty sand, (2) reed peat with a thin sand layer in the upper part, (3) clayey gyttja, (4) reed peat, (5) slightly gyttja clay, (6) moss peat, (7) clayey sand. 2A+B and 6A+B represent double samples.

Den undersökta skärningen vid Moarna nära Tvåker. Den schematiska figuren visar avlagringarnas läge i meter över nuvarande havsytan, lagernummer och uttagna prover. Resultaten av kol-14-dateringarna redovisas längst till höger. Stratigrafin av de framgrävda jordlagren är enligt följande: (1) svagt siltig sand, (2) vasstorv med ett tunnt sandskikt i övre delen, (3) lerig gyttja, (4) vasstorv, (5) svagt gyttjig lera, (6) mosstorv, (7) lerig sand, vilka illustrerats med allmänt använda symboler under "Lithology". 2A+B och 6A+B är dubbelprover.

dates on selected terrestrial material (Fig. 2). All dates mentioned in this paper are presented in radiocarbon years before the present (BP). The radiocarbon ages 5,000 BP, 8,000 BP and 10,300 BP corresponds approximately to 3,760, 7,010 and 9,600 calendar year BC respectively (Stuiver & Long 1993, Björck et al. 1996).

The nomenclature of plants follows Mossberg et al. (1992) and the Coleoptera are according to Silfverberg (1992).

Results

Ninety-eight insect taxa were identified from the ten analysed samples, together with a few remains of mites and marine polychaete worms. Beetles totally dominate the assemblages, both in number of taxa (92) and in number of individuals (Tab. 1). However, there are frequency variations between the samples (Fig. 3). Examples of some recorded beetle remains are shown in Fig. 4. Taxa of the orders Trichoptera, Hymenoptera and Diptera were also found, but they are not further presented in this paper. The insect assemblages can be described based on information concerning the species' modern biology and geographical distribution derived from Angus (1992), Bíly & Mehl (1989), Böcher (1988), Dahlgren (1979), Fitter & Manuel (1986), Fjellberg (1972), Fürsch (1967), M. Hansen (1987), V. Hansen (1968), Hansen & Henriksen (1927), Harde (1984), Landin (1957), Lekander et al. (1977), Lindroth (1985,1986), Lohse (1969), Lundberg & Gustafsson (1995), Palm (1948), Paulus (1979), Peez (1967), Silfverberg (1992) and Vogt (1967). Habitat preferences, including selected environments and food substrates, for the recorded taxa are presented in Tab. 1. A synthesis of indicated habitats concerning the beetles is shown in Fig. 5.

The major part of beetles found in all but sample eight, have today at least a part of their geographical distribution in southern Sweden. Exceptions are species such as *Bembidion normannum*, *B. iricolor*, *Badister dorsiger* and *Galerucella grisescens*, which today have their closest occurrence in Denmark or Finland.

Sample one contained very few insect remains and the recorded taxa just indicate that aquatic (Aq) and moist environments (H) existed in the study area around 5,000 BP. In samples two to seven, subfossil insects are more abundant. The

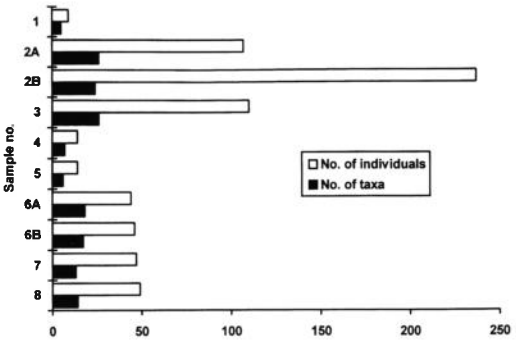

Fig. 3. Number of individuals and taxa of Coleoptera recorded in each sample.

Antal individer och taxa av skalbaggar i varje analyserat prov.

beetle assemblages suggest a relatively diverse environment, with a spectrum of different habitats, for the period ca. 5,700 to 7,800 BP. Species preferring an open landscape (O) dominate. However, obligate forest species (F) are also found in samples two and six. The presence of both deciduous (Tde) and coniferous (Tco) trees is indicated. *Adrastus pallens* is mainly phytophagous on willow (*Salix*), while *Galerucella lineola* is found on willow and alder (*Alnus*). *Dryocetes villosus* is found under the bark of oak (*Quercus*) or beech (*Fagus*). *Rhagium inquisitor* lives predominantly on coniferous trees such as pine (*Pinus*) and spruce (*Picea*), but is occasionally also found on oak. A number of taxa prefer aquatic or moist habitats. Only the record of *Amara tibialis* in sample 2B suggests dry ground (X). The majority of the hygrophilous taxa are riparian (Mw). *Stilibus oblongus* and *Donacia clavipes* are phytophagous beetles living on reed vegetation (Vr) such as common reed (*Phragmites*) and bulrush (*Typha*). *Prasocuris phellandrii* feeds on shore plants such as water dropwort (*Oenanthe*) and water parsnip (*Sium*), whereas *Galerucella grisescens* prefers *Lysimachia*. *Macroplea* species are found on the floating-leaved water plants (Vwp) such as pondweed (*Potamogeton*). *Tanysphyrus lemnae* feeds on duckweed (*Lemna*). A number of species are predominantly found in coastal environments (C) and several of these are confined to saline sites (Sa), such as salt marshes.

The insect assemblage dated to ca. 10,300 BP (sample 8) is outstanding compared with those from the other samples. It consists of species presently found in northern Fennoscandia, apart from *Simplocaria elongata* (synonymous with *S. frigida* Krogerus) which today is not found anywhere in Europe except on the Kanin peninsula. No obligate forest species (F) were recorded in the sample. The species are predominantly found in open areas (O) in arctic/alpine regions. The main part of the recorded species are aquatic (Aq), riparian (Mw) or prefer other types of moist habitats (H) such as rich fens (e.g. *Diacheila arctica*). *Helophorus glacialis* is confined to very

*Tab. 1. Taxonomic list of Coleoptera recorded from the ancient lagoon at Moarna. Species that do not belong to the modern beetle fauna in southern Sweden are indicated by *. Minimum numbers of individuals for each taxon and sample are calculated from the most abundant skeletal part. Habitat preferences, including selected environments and food substrates, of recorded taxa are indicated as: Open landscape (O), forest (F), coastal habitats (C), aquatic species (Aq), moist habitats (H), stagnant water (L), running water (R), water margins (Mw), dry habitats (X), rich fens (Rf), oligotrophic bogs (Ob), bare soils (Bs), saline habitats (Sa), grass/shrubland (Gs), tree habitats (T), coniferous trees (Tco), deciduous trees (Tde), shrubs (S), birch (+be), willows (+sx), oak (+qu), beech (+fa), herbs (Vhe), reed vegetation (Vr), water plants (Vwp), on roots (Vro), fungi (Vf), leaf litter (Ll), moss (M), dung (Du), and decaying organic matter (Do).*

*Artlista över skalbaggsfynden från den forntida lagunen vid Moarna. Arter som idag inte tillhör den sydsvenska faunan anges med *. Individantal för varje taxon i ett prov har beräknats på den kroppsdel som förekom i störst antal. Habitatkrav anges med följande förkortningar: Öppen mark (O), skog (F), kustbiotoper (C), vattenlevande (Aq), fuktig miljö (H), stillastående vatten (L), rinnande vatten (R), vid kanten av vatten (Mw), torr mark (X), rikkärr (Rf), mossar (Ob), exponerad mineraljord (Bs), salina biotoper (Sa), gräs-/buskmark (Gs), träd (T), barrträd (Tco), lövträd (Tde), buskar (S), björk (+be), sälg (+sx), ek (+qu), bok (+fa), örter (Vhe), strandväxter (Vr), vattenväxter (Vwp), på rötter (Vro), svamp (Vf), lövförna (Ll), mossa (M), spillning (Du), och multnande växt- och djurrester (Do).*

Taxon	Samples 1	2A	2B	3	4	5	6A	6B	7	8	Habitat
Carabidae, jordlöpare											
Loricera pilicornis (Fabr.)	-	-	-	-	-	-	-	1	-	-	H,F,Mw
Calosoma sycophanta (L.)*	-	1	-	-	-	-	-	-	-	-	F
Diacheila arctica (Gyllh.)*	-	-	-	-	-	-	-	-	-	1	H,Rf
Dyschirius globosus (Herbst)	-	1	-	-	-	-	-	-	-	-	He,A,Sa
Bembidion normannum Dej.*	-	-	-	-	-	-	1	-	-	-	C,Sa,Mw
B. doris (Panz.)	-	1	-	-	-	-	-	-	2	-	H,Mw,Ob
B. assimile Gyllh.	-	-	1	-	-	-	-	-	-	-	H,Mw,Vs
B. iricolor Bedel*	-	-	-	-	-	1	-	-	-	-	C,Sa,Bs
B. guttula (Fabr.)	-	-	-	-	-	-	-	1	-	-	Mw,Vs
B. mannerheimi Sahlb.	-	-	-	-	-	-	1	-	-	-	H,Fd,Mw,Ll
Pterostichus anthracinus (Ill.)	-	1	-	-	-	-	-	-	-		H,F,O,Mw
P. minor (Gyllh.)	-	1	-	-	-	-	1	-	1	-	H,Mw
P. diligens (Sturm)	-	-	-	1	-	-	-	-	-	-	H,Mw,Ob
Amara tibialis (Payk.)	-	-	1	-	-	-	-	-	-	-	C,O,X,Vs
Badister cf. *dorsiger* (Duft.)*	-	1	-	-	-	-	-	-	-	-	Fd,Mw,Ob
Dytiscidae, dykare											
Hydroporus sp.	-	-	-	-	-	-	-	1	-	-	Aq
Acilius sp.	1	1	-	-	-	-	-	-	-	-	Aq,L
Gyrinidae, virvelbaggar											
Gyrinus sp.	-	-	1	-	-	-	-	-	-	-	Aq,L
Hydrophilidae, palpbaggar											
Helophorus sibiricus (Motsch.)*	-	-	-	-	-	-	-	-	-	-	Aq,R,L
H. cf. *arvernicus* Mulsant*	-	-	-	-	-	-	-	-	-		Aq,R
H. glacialis Villa*	-	-	-	-	-	-	-	-	-	2	Aq,L
Berosus sp.	-	-	-	-	-	-	-	-	1	-	Aq,L
Enochrus subgen. *Methydrus*	-	-	-	-	-	-	-	1	-	-	Aq,L
E. sp.	-	-	-	1	-	-	1	1	-	-	Aq
Hydrobius fuscipes (L.)	-	-	1	-	-	-	-	1	-	-	Aq,R,Le
Cercyon littoralis (Gyllh.)	-	9	16	4	-	-	1	1	-	-	C,Sa,Do
C. depressus Steph.	-	31	94	25	3	-	-	1	-	-	C,Sa,Do
C. lateralis (Marsh.)	-	-	7	-	-	-	-	-	-	-	Do,Du,Ca
C. bifenestratus Küster	-	-	15	6	2	-	-	-	-	-	Mw,Bs,Vp
C. tristis (Ill.)	-	-	1	1	-	-	2	3	9	-	Mw,Do
C. sternalis (Sharp)	-	4	5	-	-	-	-	1	-	-	Mw,Do
C. spp.	-	-	21	19	2	-	-	-	-	-	-
Megasternum obscurum (Marsh.)	-	-	-	-	-	-	-	-	1		Do,Du
Hydraenidae, vattenbrynsbaggar											
Ochthebius cf. *auriculatus* Rey	-	-	-	1	-	1	2	-	-	-	Aq,L,Sa
O. cf. *minimus* (Fabr.)	-	-	3	2	-	-	2	-	-	-	Aq,Le
Ptiliidae, fjädervingar											
Ptenidium sp.	-	-	-	-	1	-	-	-	-	-	Do
Silphidae, asbaggar											
Phosphuga atrata (L.)	-	-	-	-	-	-	-	1	-	-	F,T
Staphylinidae, kortvingar											
Quedius spp.	-	4	-	-	-	1	1	-	-	-	H,Do,Ll,M
Xantholininae indet.	-	17	-	-	-	-	-	1	5	-	-
Paederinae indet.	-	-	18	-	-	-	-	-	-	-	-
Stenus spp.	-	-	1	1	-	-	1	1	-	1	H,Mw
Omalium riparium Thomson	-	15	29	12	1	-	2	-	-	-	C,Do,Ca
Olophrum fuscum (Grav.)	-	-	-	-	-	-	-	-	-	10	H,Mw,M
O. boreale (Payk.)*	-	-	-	-	-	-	-	-	-	1	H,Mw,Ll,M
Eucnecosum cf. *brachypterum* (Grav.)	-	-	-	-	-	-	-	-	-	6	H,Mw,Ll
Acidota crenata (Fabr.)	-	1	-	-	-	-	-	-	-	-	H,Ob,Ll*A.*
A. cruentata (Mannh.)	-	1	-	-	-	-	-	-	-	-	H,Do,Ll
Boreaphilus henningianus Sahlb.	-	-	-	-	-	-	-	-	-	2	Gs,Ll,Mw,M
Tachinus sp.	-	-	-	-	-	-	1	-	-	-	-
Aleocharinae indet.	-	2	6	3	-	-	-	-	1	2	-
Gen. indet.	1	-	-	19	-	-	-	-	-	-	-

Continued

Taxon	Samples 1	2A	2B	3	4	5	6A	6B	7	8	Habitat
Histeridae, stumpbaggar											
Hypocaccus metallicus (Herbst)	-	-	1	-	-	-	-	-	-	-	C,Bs
Scirtidae, mjukbaggar											
Cyphon spp.	5	-	8	2	1	-	2	3	3	-	Aq,Vwp
Scarabaeidae, bladhorningar											
Aegialia arenaria (Fabr.)	-	-	-	1	-	-	-	-	-	-	C,Bs
Aphodius spp.	-	1	1	-	-	-	-	-	-	-	Du
Phyllopertha horticola (L.)	-	1	-	-	-	-	-	-	-	-	T,Vl,Vro
Elateridae, knäppare											
Athous subfuscus (Müll.)	-	1	-	-	-	-	-	-	-	-	F
Agriotes sp.	-	-	-	1	-	-	-	-	-	-	Vr
Dalopius marginatus (L.)	-	-	-	-	-	-	1	-	-	-	F
Adrastus pallens (Fabr.)	-	-	-	-	-	-	-	-	1	-	Tsx
Byrrhidae, kulbaggar											
Simplocaria cf. *elongata* Sahlb.*	-	-	-	-	-	-	-	-	-	1	M
S. metallica (Sturm)*	-	-	-	-	-	-	-	-	-	5	M
Byrrhus sp.	-	-	-	1	-	-	-	-	-	-	M
Curimopsis cf. *nigrita* Palm	-	-	-	-	-	-	1	-	-	-	H,M
Nitidulidae, glansbaggar											
Epuraea sp.	-	-	-	1	-	-	-	-	-	-	Tfu
Sphindidae, slemsvampbaggar											
Aspidiphorus orbiculatus (Gyllh.)	-	-	-	-	-	-	-	-	1	-	Vf
Cryptophagidae, fuktbaggar											
Atomaria sp.	-	-	-	1	-	-	-	-	-	-	Do,Mw
Gen. indet.	-	6	3	2	-	-	-	1	-	-	Do
Phalacridae, sotsvampbagggar											
Olibrus cf. *corticalis* (Panz.)	1	-	-	-	-	-	-	-	-	-	Vhe
Stilibus cf. *oblongus* (Erich.)	-	-	-	-	-	-	1	-	-	-	H,Vr
Coccinellidae, nyckelpigor											
Hippodamia variegata (Goeze)	-	-	-	1	-	-	-	-	-	-	H,Vr
Latridiidae, mögelbaggar											
Cartodere constricta (Gyllh.)	-	-	-	1	-	-	-	-	-	-	H,Do
Colydiidae, barkbaggar											
Bitoma crenata (Fabr.)	-	1	-	-	-	-	-	-	-	-	T
Anthicidae, snabbaggar											
Anthicus ater (Panz.)	-	1	-	1	-	-	-	-	-	-	Do
A. antherinus (L.)	-	-	1	-	-	-	-	-	-	-	Do
Omonadus cf. *formicarius* (Goeze)	-	1	-	-	-	-	-	-	-	-	Do
Cordicomus instabilis (Schmidt)	-	2	-	-	-	-	-	-	-	-	Do
Cerambycidae, långhorningar											
Rhagium inquisitor (L.)	-	1	-	-	-	-	-	-	-	-	Tco
Chrysomelidae, bladbaggar											
Macroplea appendiculata (Panz.)/*mutica* (Fabr.)	-	-	-	-	4	9	22	26	-	-	H,Vwp
Donacia clavipes Fabr.	1	-	-	-	-	-	-	-	-	-	H,Vr
Prasocuris phellandrii (L.)	-	-	-	-	-	-	-	-	1	1	H,Vr
Chrysomela collaris L.	-	-	-	-	-	-	-	-	-	1	Ssxbe
Galerucella cf. *grisescens* (Joan.)*	-	-	-	-	-	-	1	1	-	-	H,Vr
G. cf. *lineola* (Fabr.)	-	-	-	1	-	-	-	-	-	-	Tde
Galeruca tanaceti (L.)	-	-	-	-	-	1	-	-	-	-	Vhe
Luperus longicornis (Fabr.)	-	1	-	-	-	-	-	-	-	-	Vro
Chaetocnema sp.	-	-	-	1	-	1	-	-	-	-	Vhe
Apionidae, spetsvivlar											
Apion spp.	-	1	1	1	-	-	-	-	-	-	Vhe
Curculionidae, vivlar											
Tanysphyrus lemnae (Payk.)	-	-	-	-	-	-	-	-	2	-	H,Vwp
Ceutorhynchus sp.	-	-	-	-	-	-	-	-	1	-	Vhe
Scolytidae, barkborrar											
Dryocoetes cf. *villosus* (Fabr.)	-	-	1	-	-	-	-	-	-	-	Tqufa

*Fig. 4. A portion of beetle remains found in the sediments of the ancient lagoon at Moarna, Tvåker, SW Sweden. The picture shows elytra, thoraces, head and legs of ground beetles, water scavenger beetles (**Cercyon** spp.), rove beetles and true weevils from sample 2A. Photo: G. Lemdahl.*

*Exempel på skalbaggsrester funna i sedimenten från forntidslagunen vid Moarna nära Tvåker. Bilden visar täckvingar, halssköldar, huvud och ben av jordlöpare, palpbaggar (**Cercyon** spp.), kortvingar och vivlar funna i prov 2A.*

cold stagnant water (L), such as meltwater from snow patches or glaciers. Several of the rove beetles (Staphylinidae) are common in leaf litter (Ll) from dwarf shrubs of willow and birch (*Betula*), and *Chrysomela collaris* is a phytophagous beetle feeding on the leaves of that type of vegetation.

Discussion

It is interesting to compare the occurrence of species in the fossil assemblages with the present fauna in the study area (Gustavsson unpublished). Species such as *Cercyon littoralis* and *Omalium riparium* are very common today along the seashores, particularly in drift of seaweed (*Fucus*) or other types of decaying plant litter. *Hypocaccus metallicus* and *Aegialia arenaria* are today character species of the coastal sand dunes. These four species seem also to have been relatively frequent in the area during the period ca. 8,000 to 6,000 BP. However, *Cercyon depressus* and *C. sternalis* which are numerous in samples 2 and 3, are rarely found in the area today. *Ochtebius auriculatus* is rare throughout Scandinavia today. In North Europe it only occurs with any frequency in SW Denmark. In Sweden it has only been recorded from a few localities, including sites in the province of Halland. Species of the genus *Macroplea* have rarely been found in the study area, but may be disregarded because they are difficult to collect (Nilsson 1996).

Moreover, there are species in the fossil assemblages that have not previously been recorded

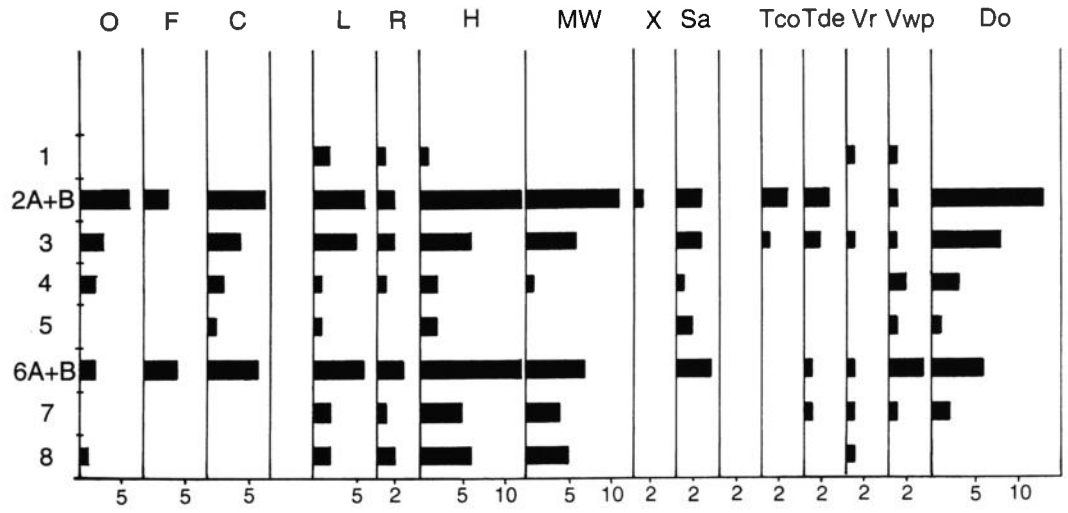

Fig. 5. Habitat and food substrate preferences of recorded Coleoptera. Number of taxa selecting open landscape (O), forests (F), coastal habitats (C), stagnant waters such as lakes and ponds (L), running water (R), moist environments (H), water margins (MW), dry ground (X), saline sites (Sa), coniferous trees (Tco), deciduous trees (Tde), shore vegetation (Vr), floating-leaved water plants (Vwp), and decaying organic matter (Do). A taxon may indicate more than one environmental factor.

Habitat- och födosubstratpreferenser hos de listade skalbaggarna. Staplarna visar antal taxa som trivs i miljöer som: öppen mark (O), skogsmark (F), kustmiljöer (C), sjöar och dammar (L), rinnande vatten (R), fuktiga platser (H), vid kanten av stillastående eller rinnande vatten (MW), torr mark (X), salina biotoper (Sa), barrträd (Tco), lövträd (Tde), strandväxter (Vr), flytbladsväxter (Vwp) och multnande växt- och djurrester (Do). Ett taxon kan ange mer än en miljöfaktor.

from the province of Halland and in some cases not in the whole area of southern Sweden either. Only a few single finds of *Calosoma sycophanta* are reported from southern Sweden during modern time and it is probably not resident in Scandinavia or Denmark today. This subfossil record of the species together with other more or less contemporary records (Lindroth 1942, Welinder 1970) may suggest that it belonged to the Swedish fauna at least around 5,000 BP. *Bembidion normannum* and *B. iricolor* have their northern European distribution limit in SW Denmark, where they are found along the tidal coast. *Pterostichus anthracinus* is rare today in southern Sweden, except on the islands of Öland and Gotland (SE Sweden) where it is common. *Badister dorsiger* which may have lived at the margin of the ancient lagoon, is today closest found in southern Denmark, where it is very rare, predominantly inhabiting forest swamps or the borders of shaded temporary pools in deciduous forests. In north Europe *Galerucella grisescens* is today only recorded in Finland, Karelia and the Baltic nations. Around 7,000 BP it may have dwelled in coastal environments in southwestern Sweden. Other species that have not previously been recorded from the province of Halland are *Cartodere constricta* and *Cordicomus instabilis*.

The reasons for the extinction of a number of species in the study area are most likely changes in climate, local environment and/or human impact. Extinction caused by climatic change is evident concerning the disappearance of the arctic/alpine fauna recorded in sample 8. This type of fauna dominated during the major part of the Late-glacial period (ca. 13,000 - 10,000 BP) in southern Sweden according to subfossil insect records obtained from a number of sites (Lemdahl 1997). Around 10,000 BP a very rapid and marked faunal change is indicated. The arctic/subarctic insect fauna, which probably moved north to the retreating ice margin in southern central Sweden,

was replaced by species found in southern Sweden today. This faunal change was most likely a response to a contemporary strong climatic amelioration, when mean summer temperatures rose rapidly by 6 to 7°C and mean winter temperatures even more (Berglund et al. 1994). The occurrence of species such as *Calosoma sycophanta*, *Bembidion normannum*, *B. iricolor* and *Badister* cf. *dorsiger* in samples 2, 5, and 6 may partly indicate a slightly warmer climate during the Middle Holocene compared with today. However, their required habitats may also have been more common during that period and provided populations large enough for the survival of species today extinct in area. Sea-level rises along both the Swedish west coast and the Baltic coast in southern and south-east Sweden (Gaillard et al. 1988, Gaillard & Lemdahl 1994) evidently caused the formation of lagoons and environments that presently have no analogs in southern Scandinavia. The palaeoecological results suggest that the vegetational and faunal diversity in these types of environments were relatively high, providing a large spectrum of different habitats. The lifetime of these lagoons seems in general to have been less than ca. 3,000 years. In the case of the lagoon at Moarna the limnic sedimentation ceased around 6,000 BP and it developed into a reed swamp. At ca. 5,000 BP the swamp was covered by aeolic sand that formed dunes.

Changes in the faunal diversity are indicated during the period ca. 7,500 to 5,000 BP (Fig. 3). They could be ascribed either to changes in the local environment or taphonomical (processes that affect an organism after death) reasons, such as changes in accumulation of insect remains in the sediment. The deviating high number of taxa at sampling levels 2A+B and 6A+B are more likely due to the doubled sample size than to a higher degree of faunal diversity. It is a well known phenomenon that the number of taxa increases with larger sample volumes. However, the decrease in both number of taxa and individuals in samples 4 and 5 may be due to a temporary disappearance of habitats locally in the area. However, no change in the lithology that may indicate an environmental change is traced at these particular levels. The shift in faunal diversity from sample 2 to 1 is on the other hand coupled with distinct lithological change. The change from clayey gyttja to a reed peat indicates that the lagoon was transformed into a reed swamp. The rapid Tapes transgression and the later subsequent regression (Påsse 1990) may have been locally destructive and generative respectively to the coastal environments.

Conclusions

The present study of course gives a very limited view of the total insect or beetle fauna in the study area during the time period considered. However, even this little peep-hole into ancient time gives surprisingly interesting and valuable information concerning certain beetle species that today are very rare or locally/regionally extinct. More systematic studies at similar sites along the south-western coast of Sweden would probably help to supplement our knowledge of these relatively temporary and unique lagoon ecosystems. Such knowledge may contribute to both nature conservancy and studies of species diversity.

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Sammanfattning

Vid grävarbeten för en ny järnvägsdragning frilades sjösediment- och torvavsättningar vid Moarna nära Tvååker vid Hallandskusten. Liknande avsättningar är vanliga längs stora delar av den halländska kusten. De har vanligen avsatts i laguner som bildats när havsnivån stigit under särskilda tidsperioder. En av dessa havsnivåförandringar kallas Tapestransgressionen och ägde rum för mellan ca 8 000 och 6 000 år sedan (BP) (Påsse 1983). Avsättningarna visade sig vara relativt rika på insektrester, varför vi beslöt att göra en mer ingående undersökning av dessa. 98 olika insekttaxa kunde utpreppareras och bestämmas ur tio analyserade jordprover. Av insekterna utgörs inte mindre än 92 taxa av skalbaggar (Tab. 1).

Djurfynden anger att den forntida lagunen hyste ett stort antal skalbaggsarter beroende på en rik förekomst av olika habitat. Liknande fornmiljöer har undersökts längs Östersjökusten i Skåne (Lemdahl 1988a, Gaillard et al. 1988, Gaillard & Lemdahl 1994), vilka uppvisar likartade förhållanden. Sammantaget visar undersökningarna på artrika ekosystem som saknar någon motsvarighet i Sydskandinavien idag. Flera av fynden utgörs av arter som numera är försvunna ur den halländska skalbaggsfaunan eller är sällsynta. Exempel är *Pterostichus anthracinus, Cercyon sternalis, Ochthebius auriculatus, Cartodere constricta* och *Cordicomus instabilis*. Andra arter som t.ex. *Calosoma sycophanta, Bembidion normannum, B. iricolor* och *Galerucella grisescens* saknas i Sydsverige idag. De påträffas närmast i sydligaste Danmark eller Finland. Bottenprovet (8), i torv, innehåller djur som lever i arktiska miljöer. *Diacheila arctica, Helophorus sibiricus, H. glacialis, Olophrum boreale* och *Simplocaria arctica* finns idag närmast i nordligaste Fennoskandien. Dessa arter och andra arktiska/subarktiska djur var dock vanligt förekommande i Sydsverige mellan ca 13 000 och 10 000 BP (Lemdahl 1996). Det eventuella fyndet av *Simplocaria elongata* är intressant då denna kulbagge idag närmast lever på Kaninhalvön i Nordryssland.

Även om denna undersökning inte ger en på något sätt komplett bild av den forna skalbaggsfaunan i undersökningsområdet vid Hallandskusten nära Tvååker, så är den ändå ett värdefullt bidrag till förståelsen av icke längre existerande miljöer och faunahistorien. Vidare anser vi att mer systematiska undersökningar av liknande fornlaguner längs Västkusten kan avsevärt öka vår kunskap om dessa relativt kortlivade ekosystem (ca 3 000 år), en kunskap som borde vara värdefull både i naturvårdshänseende och för forskning om biologisk mångfald.